

Biotic and abiotic factors affecting
Saccharina latissima, survival, growth
and recruitment

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IV

Abstract

There has been a rising concern for the large decline of *Saccharina latissima* along the southern coast of Norway. Increasing summer temperatures leads to altered turf cover, loaded with sediments, and darkening of the coastal waters. The aim of this study was to monitor the recruitment and growth of *S. latissima*, to analyze the factors affecting its distribution. This study was conducted at six stations in the skerries of Grimstad, Norway. This area is characterized by a sheltered inner skerries and a more exposed outer skerries. Thus, reflecting a wave exposure gradient. The life stages of *S. latissima* were observed in summer and fall 2016, and summer 2017. Moreover, the amount of sedimentation and turf was monitored, and turf samples were collected and analyzed. Transplanted sugar kelp was planted at every station to monitor growth and survival. Temperature and light data was also recorded, using a HOBO-logger. Statistical analyses (GLM) were conducted on recruitment in relation to sedimentation and turf cover.

This study revealed that high summer temperatures in 2016 might have caused a great loss of individuals among the transplanted *S. latissima*, and a prominent decline in the presence of adult individuals at every station. The general abundance of both adult individuals and recruits, increased with higher wave exposure. Turf and sedimentation tended to decrease with increasing wave exposure which indicate a clear impact on the recruitment. The species composition of turf displayed little difference among stations, but the diversity declined with increasing exposure. Light availability varied between stations and the most exposed stations had the lowest light availability which was not expected. However, this had little effect on growth. These data provided important insight into the response of *S. latissima* on different biotic and abiotic factors in a changing environment. Global warming may continue to increase ocean temperature and this could make southeast Norway a less preferred area for the species.

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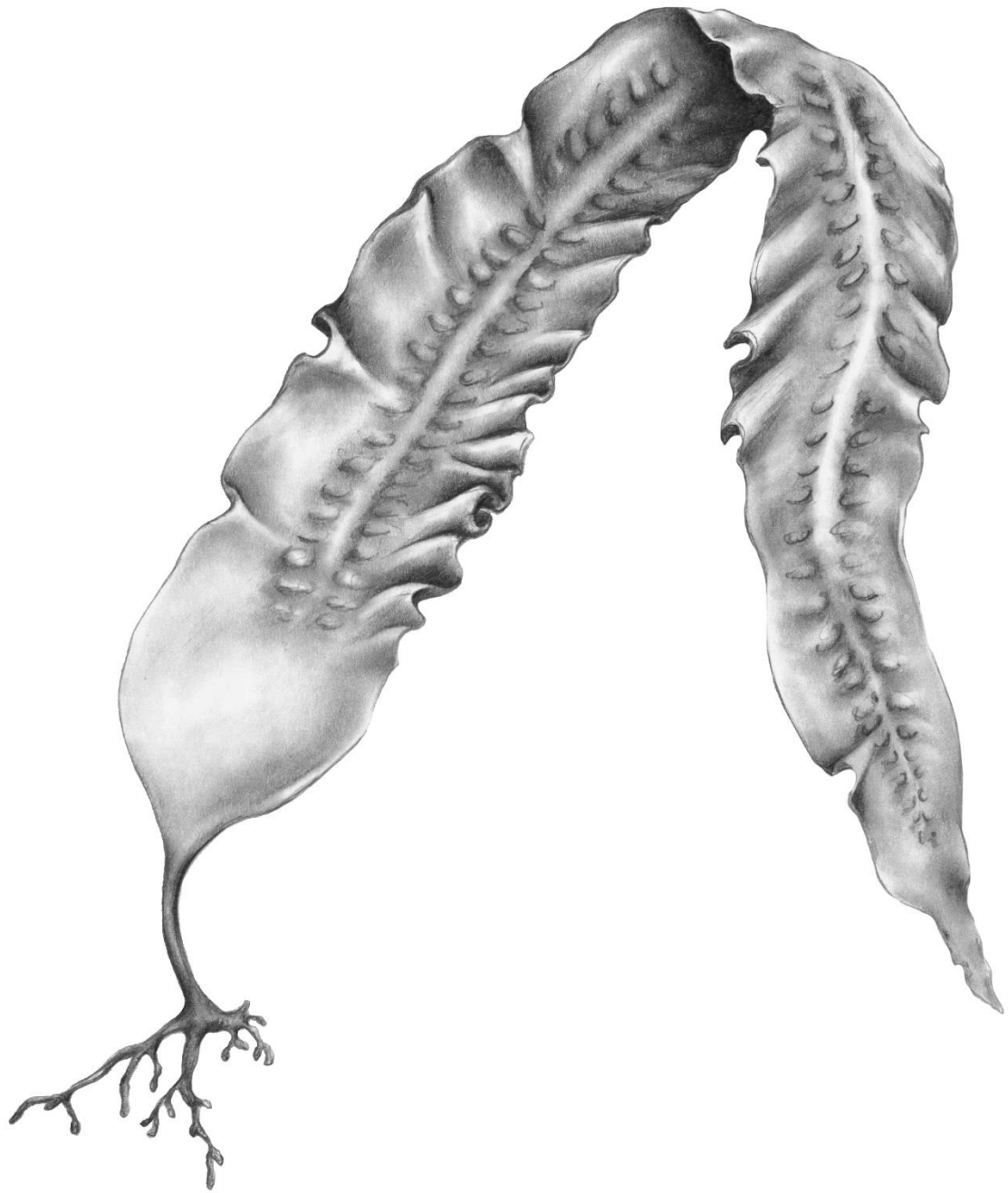


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1 Introduction

1.1 *Saccharina latissima* in a changing environment

The sugar kelp, *Saccharina latissima* (L.) C. E. Lane, C. Mayes, Druehl & G.W. Saunders represent an important part of the Skagerrak flora. This is a perennial kelp providing a three-dimensional habitat giving shelter and protection for other algae and animals (Christie et al., 2009). Also a large number of predatory fish seek their prey in kelp forests (Norderhaug et al., 2005). Moreover, as *S. latissima* is a primary producer, it also contribute with potential nutrition for consumers (Christie et al., 2009). Thus, the sugar kelp ecosystems are complex, include many trophic levels and preserve a high biodiversity.

When opportunistic turf algae outcompete *S. latissima*, the species richness decrease as the turf, in contrast to sugar kelp, is annual. The barren grounds contribute with little protection for small fish and invertebrates. This can potentially have a cascading effects on the food web (Eriksson et al., 2002). Sugar kelp maintains a stable environment, thereby sustaining a higher biodiversity.

S. latissima has during the last two decades had major setbacks along the southern Norwegian coast, from Oslo to Bergen (Moy, 2006). In light of ongoing global climate change and eutrophic tendencies in Skagerrak, this has raised great concern among the scientific community, and The Norwegian Environmental Agency have funded several projects (e. g. Gundersen et al., 2014; Moy et al., 2009; Norderhaug et al., 2011). On the basis of this, The Norwegian Biodiversity Information Centre categorized the species as near threatened and the species was red listed in 2010, but later removed (2016), as the distribution slightly improved.

However, during the first project, Sukkertareprosjektet (2005 – 2008), the scientific surveys revealed a setback of *S. latissima* in the order of 80% on the Norwegian south coast, and 40% on the Norwegian western coast (Moy et al.,

2009). This serious decline led to an ongoing monitoring of *S. latissima*, and further investigation on all the factors affecting its distribution (e. g. Moy et al., 2017; Norderhaug et al., 2013). Due to the complexity of the community dynamics, it has shown to be difficult to identify factors responsible for the reduction. According to Moy et al., (2009) the most important factors influencing *S. latissima* distribution includes temperature, light transparency, nutrient concentration, and competition with other species. But their relative importance and deciding influence, remains somewhat unknown.

1.1.1 Biology

S. latissima is a temperate to polar macroalga, being widely distributed on the northern hemisphere (Kain, 1979). On the east Atlantic coast, it can be found in the sub-tidal zone from Portugal to the polar regions of Norway, including Svalbard. The species prefer semi-exposed to sheltered habitats attached to rocky substrate, and can be found between 1 – 30 meters, although usually dominating the upper parts (Moy and Christie, 2012). The adaptation to the semi-exposed habitats is clearly seen in the species morphology, characterized by strong holdfast that retains a firm grip to the substrate (Kain, 1979). The species great dominance and wide distribution along the Norwegian coast indicates a high adaptation to the temperate and cold conditions dominating this coast (Sjøtun and Schoschina, 2002).

The vegetative growth of sugar kelp starts during winter, and throughout the early spring the sugar kelp utilizes the energy, in form of chrysolaminaran, conserved during the summer. This is an advantage, as they don't depend on light and can therefore allocate their reserves for optimal growth during late winter and early spring, when inorganic nutrients are available in the water masses. The species has an intercalary meristem, meaning that their growth appears between the stipe and the blade. As the oldest tissue is on the outer tip of the blade, it is gradually eroded away when the algae grows (Andersen et al., 2011). The expected life span is 1 – 4 years, and individuals may reach 3 m in length (Christie et al., 2009).

S. latissima has a diplohaplontic life cycle which is characterized by two morphologically different stages (Fig. 1). In the autumn and winter, adult kelp releases haploid spores which germinate into microscopic male and female gametophytes, fixing themselves to a rocky clean substrate (Schiel and Foster, 2006). The male gametophyte releases spermatozooids that fertilize the eggs on the female gametophyte (Bartsch et al., 2008). By this fertilization the sugar kelp enters the diploid stage in their life cycle. The sporophyte will develop from the fertilized egg and as the spring unfold, the germinating sporophyte will gain length while the female gametophyte disintegrate (Kain, 1979). During the first summer, new sporophytes may reach one meter in length, but still they have to wait for another year to become a mature fertile individual. The first growth season is critical, since they have no internal nutrient reserves and is therefore dependent on photosynthesis to survive (Tranum et al., 2012).

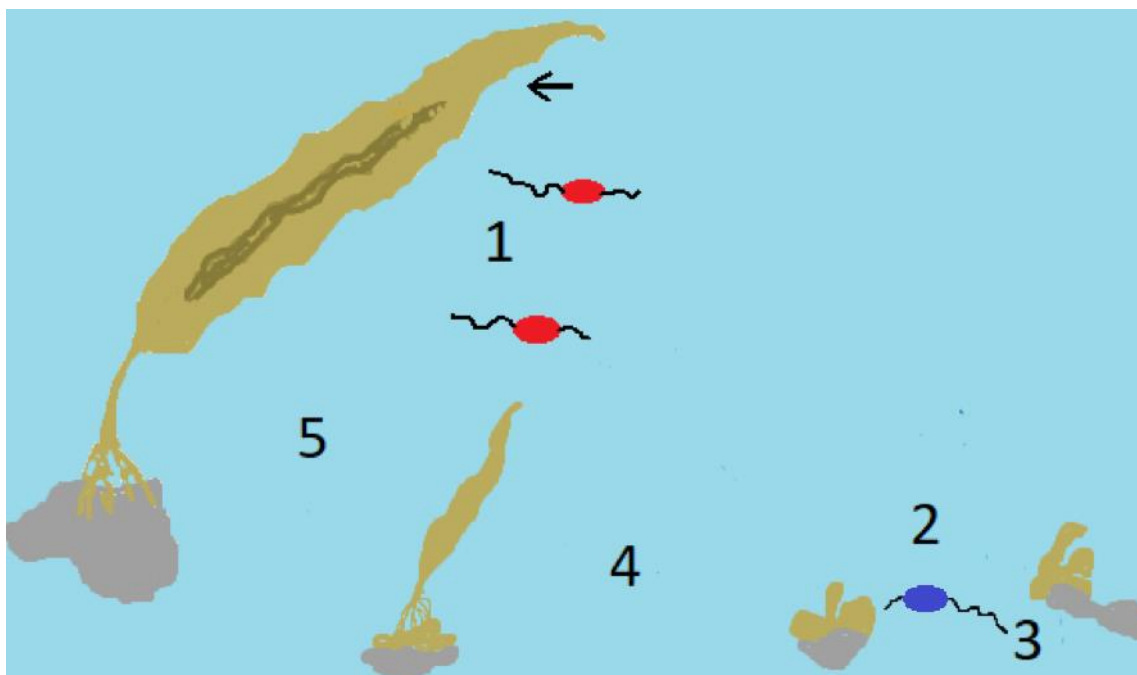


Figure 1: Illustration of *S. latissima* diplohaplontic, heteromorphic life cycle. 1: Release of haploid zoospores from sori (black arrow) on adult sugar kelp. 2: Zoospores attaches to rocky substrate and germinate into microscopic male and female gametophytes. 3: Male gametophyte releases spermatozooids, which fertilize an egg on the female gametophyte. 4: The fertilized egg germinates into new sporophyte. 5: During spring the young algae grow into an adult sugar kelp.

1.2 Influential factors

Wave exposure is driven by the prevailing system of winds and ocean currents. On the inner coast, these movements are limited due to skerries (Moy et al., 2009). This means that compared to the more exposed areas, the terms for competition is likely to be different in these more sheltered areas, mainly due to physical stress (Fenwick, 1976; Jørgensen and Christie, 2003). However, as many other environmental conditions are changing in the southern coast of Norway, sugar kelp is struggling to maintain its dominant abundance (Moy and Christie, 2012; Moy et al., 2009). Thus, a large scale shift from sugar kelp to turf has been reported on the inner coast (Moy et al., 2009; Norderhaug et al., 2011). The term turf covers a diverse group of macroalgae. They are defined as fast growing species providing little physical structure, and being very stress tolerant (Airoldi, 1998). To better understand the effects on *S. latissima*, it is important to investigate the environmental factors that have recently changed. Therefore, I will now present the most important environmental factors, and discuss their influence on the sugar kelp distribution in southern Norway.

1.2.1 Temperature

Bolton and Lüning (1982) showed that the optimum temperature for *S. latissima* is between 10 – 15°C. Furthermore, Lüning (1980) revealed that the distribution is mainly determined by summer temperatures. A steady increase in the ocean temperature has been recorded in the Skagerrak Sea during the period from 1960 – 2009. Especially during the summer of 1997, 2002 and 2006 extreme summer temperatures were recorded several times over longer periods (Andersen et al., 2011). The summer of 1997 is thought to be a critical year for the sugar kelp, with temperatures reaching 19°C or above for more than two months (Moy et al., 2009).

Laboratory observations have revealed that when the ocean temperature becomes too high, Norwegian sugar kelp will spend more energy on respiration than what they are able to generate through photosynthesis. This increase in metabolism will

deplete their reserves and they will become more vulnerable (Andersen et al., 2013). Andersen et al. (2013) showed that when *S. latissima* is retained at 20°C over time, they start to show evidence of reduced photosynthetic ability. In addition, Bolton and Lüning (1982) demonstrated that sugar kelp can only sustain 23°C for a few days before dying. Thus, changes in temperature will reduce sugar kelps resilience, and the presences in south Norway may become unstable.

Another consequence of changing temperatures is an advantage to competitors. In contrast to sugar kelp, turf benefits from high water temperatures, and may rapidly achieve vegetative dominance (Lotze and Worm, 2000).

1.2.2 Light

Since *S. latissima* is depended on a minimum of solar radiation to maintain adequate photosynthesis, the lower limit of its distribution is determined by the light conditions (Moy and Christie, 2012). In southern Norway, the depth distribution has been reduced during the last 60 years; from 25 to 12 meters (Moy et al., 2009). This change in distribution is correlated to the observed increase in light attenuation in the Norwegian Skagerrak Sea, with a corresponding gradual reduction in transparency during the 20th century (Aksnes et al., 2009).

A gradual increase of the ocean temperature and the amount of precipitation and subsequent run-off from land are the indirect factors causing the reduced light penetration. During the winters in Norway the fresh water and nutrients are usually bound up in ice. In absence of frost, there will be a continuous supply of fresh water and nutrients from the rivers bringing large amount of particulate organic matter (POM) and dissolved organic material (DOM) into the coastal waters. Subsequently, the water transparency will be reduced, and this darkening will alter the depth distribution of sugar kelp (Aksnes et al., 2009; Kemp et al., 2005).

1.2.3 Turf

The retreat of perennial sugar kelp forest along the southern coast of Norway is increasing. The species is being replaced by annual turf (Moy and Christie, 2012). It is believed that these changes must have occurred in the years just after 1996, since after this year, the kelp has never been reported to dominate (Christie, 1997; Moy, 2006). Although turf will be grazed upon by snails and other invertebrates, this predation pressure is too low to reduce its dominance (Worm and Lotze, 2006). Since turf also tend to accumulate sediments. This makes the bottom cover even more dense (Connell et al., 2014).

One of the reasons why sugar kelp struggles to regain its dominance, is that the turf over-grow their germinating spores in the early spring. When the juvenile *S. latissima* is covered by turf during the summer, their photosynthesis will be prevented (Schiel et al., 2006).

1.2.4 Sedimentation

It has been reported that the amount of sediment covering the rocky habitats has a great impact on kelp recovery (Gorman and Connell, 2009). Large amounts of filamentous turf, covering the bottom flora, also have the ability to bind sediments which could further complicate recruitment for *S. latissima* (Moy and Christie, 2012). The climate change with increasing temperatures affects both abiotic and biotic processes in the ocean. Furthermore, a secondary outcome of eutrophication is an altered sedimentation rate (Cossellu and Nordberg, 2010). Since the 1980s, this increase has been measured to near 40% (Moy et al., 2009). The sediments consist of different waste products and other particles originating from fresh water input (Cossellu and Nordberg, 2010; Moy et al., 2008). These particles will sink down from the surface area, down to the bottom and cover the rocky substrate. It is especially the recruitment of sugar kelp which is vulnerable because the spores are not able to attach properly (Andersen, 2013b), and germinating spores may be prevented from their required sunlight (Isæus et al., 2004). These effects have a negative impact on the recruitment.

1.2.5 Eutrophication

All the factors describe above are all tightly connected to eutrophication. High input of nutrients into marine ecosystems can lead to excessive bloom of opportunistic macroalga, toxic phytoplankton blooms and anoxic conditions for the bottom fauna (Skogen et al., 2014; Smith et al., 1999). These features are all recognized as main characteristics of eutrophic processes, which suppress natural flora and fauna, and reduces biodiversity.

The Skagerrak Sea is classified as over-fertilized and exhibits eutrophic characteristics. The most prominent sign is the growth of turf and high oxygen consumption in the deeper fjords (Moy et al., 2009).

The nutrient supply comes mainly from local resources with land areas dominated by urbanization and agriculture. All the drainage from these areas gathers in bigger rivers, accumulating large amounts of nutrients. Some of Norway's largest rivers have their estuaries on the southern coast, mainly from Oslo to Stavanger, which makes these areas especially affected by eutrophication (Moy et al., 2008). Skagerrak is continuously influenced by ocean currents from The Baltic Sea, the southern North Sea and The Atlantic Sea, but these ocean currents constitute only a secondary aspect of the nutrient supply. The amount of nutrients in these currents culminated in 1995, and has subsequently decreased back to 1980 levels, therefore reducing their effect on eutrophication (Aure and Magnusson, 2008). That is why the local aspect is highly relevant. Obtaining knowledge regarding these regional conditions and how they develop is vital to pass through corrective means.

1.3 Aims and hypotheses

It has previously been reported in southern Norway that the abundance of *S. latissima* is decreasing on the inner coast relative to the outer coast. The various factors presented above, plays a key role affecting the distribution of the species. Thus, the change in these factors and their individual effect is uncertain, together

representing a complex system (Andersen et al., 2011; Moy and Christie, 2012; Moy et al., 2009; Norderhaug et al., 2013). The aim of this study was to investigate how *S. latissima* is influenced by various stressors related to temperature and eutrophication from the inner coast to the outer skerries around Grimstad in southern Norway. By comparing the distribution with environmental data, my aim for this thesis was to gain insight in the factors causing the reduction of sugar kelp communities in southern Norway. Specifically, I have tested the following hypotheses:

H1: High summer temperatures has a negative influence on *S. latissima* survival

H2: Poor light conditions have negative effects on *S. latissima* growth and recruitment

H3: Turf and sedimentation has negative effects on *S. latissima* recruitment

2 Material and methods

2.1 Study area

The fieldwork was conducted at six different locations in the archipelago of Grimstad (Fig. 2). Grimstad is located in southern in Norway, lying central in the Skagerrak Sea. It mainly receives oceanic influxes from the southern part of The North Sea, The Baltic Sea, but also from The Atlantic Sea. Both The Baltic Sea and The Skagerrak sea are influenced by many rivers running through agricultural and urban areas. In Skagerrak in the outer Oslofjord, Norway's biggest rivers, Glomma and Drammenselva, have their estuaries, as well as many other smaller rivers further down the Norwegian south coast (Moy et al., 2009). These river outputs contributes to a lowered salinity in The Skagerrak Sea, compared to the Atlantic Ocean (Sætre and Ljøen, 1972). The Norwegian coast is characterized by many skerries which can reduce the water exchange, especially on the inner coast (Gundersen et al., 2014). Grimstad represents such conditions, by having both inner and outer skerries.



Figure 2: Overview of study area. Each station is marked (see red dot) with its associate station name. Grey dotted line indicate the sill in Groosefjorden.

2.2 Sampling design

Most stations were established for this project (SA1, SA2, SA3 and SA4), while two (HB6 and HB7) have previously been used by Norwegian Institute for Water Research (NIVA) as part of a monitoring program (Trannum et al., 2012). Station HB6, SA3 and SA4 are all within the inner part of the skerries, being slightly more protected (Fig. 2). This part is called Goosefjorden. Outside of the sill is station HB7, SA1 and SA2 surrounding Homborsund. This is a more exposed area, having an open connection to the Skagerrak sea (Jacobsen et al., 1997). Such an arrangement provides an exposure gradient. This is important factors which has many implications on both biological and environmental aspects (Norderhaug et al., 2012). I will now introduce the biological and environmental factors sampled in this study, and pair them with my hypotheses (Table 1).

Table 1: Overview of all observations and data collection during fieldwork.

Factors	Methods	Hypotheses
Biological	Measuring density and life stages of <i>S. latissima</i> in a quadrat	H1, H2 and H3
Biological	Transplantation of adult sugar kelp: survival and growth (puncture method)	H1, H2
Biological	Local sugar kelp: survival and growth (puncture method)	H1, H2
Biological	PAM-data: interpret <i>S. latissima</i> physiological state	H2
Biological	Turf community: sample turf flora and identify species	H3
Environmental	Temperature: is there any extreme values during the summer season	H1
Environmental	Light availability: is there adequate light conditions for growth	H2
Environmental	Sedimentation: does the amount reduce <i>S. latissima</i> recruitment	H3

2.3 Biological responses

2.3.1 Sampling

Sampling was conducted during two different seasons, early summer and late fall. Summer is optimal for registration of recruitment. Two rounds of sampling were carried out for the summer seasons, mid-June 2016 and mid-June 2017, and one sampling for the autumn season, late October 2016. A field trip during summer 2017 was carried out to measure survival and growth rate of the transplanted sugar kelps during the winter season, but also the recruitment, which happens during winter/early spring. The turf cover was also measured in the autumn, when turf is at its most developed.

2.3.2 Sugar kelp population structure

Measuring the density and life stages of sugar kelp was conducted by placing a 1 m² quadrat randomly on the sea floor, four times at each station. Within each frame all the different life stages of present *S. latissima* were counted: seedlings, juveniles (< 10 cm) and adult sugar kelp. The percent cover of sediment, bare rock and fast-growing algae were noted visually.

2.3.3 Growth and survival - Transplanted sugar kelp

Adult and healthy sugar kelps were brought in from station SA1, and attached to a rope and a heavy metal chain at 8 m depth at every station (Fig. 3). In total 30 adults were collected with five individuals at each station. The aim was to see if these transplanted sugar kelps were able to grow and survive. Especially on the most sheltered stations with little or no local sugar kelp. To mark the algae, a yellow cable tie was put around the stipes. For growth measurements two small holes were gently punched in the lamina, one hole 10 cm above the meristematic transition zone, and another 20 cm above.



Figure 3: Transplanted sugar kelp was attached to a rope and a heavy chain to keep its position. The yellow cable tie is not yet put on in this photo. Photo: NIVA.

2.3.4 Growth and survival - Local sugar kelp

Local sugar kelp plants at each station were also marked and punched, similar to the transplanted individuals. The presence of local sugar kelp varied between stations, but this made it possible to study local variation in growth and survival, and to see the development of the transplanted sugar kelp on stations with no local sugar kelp.

2.3.5 Turf community

The amount of turf cover at each station was determined by eyesight using the same quadrat (1 m²) as in the measuring of the population structure. The amount was defined in percentage. Additionally, at all stations, a 25 cm² frame were cleared free of algae and animals (Fig. 4). The content was put in a bag under water, later transferred to a 1000 ml plastic jar on land and formalin was added to prevent bacterial degradation. Two sample was collected for each station, summer and fall 2016. This resulted in 12 samples in total. The species composition in each sample was examined in lab. The frames, being cleared at every fieldtrip in 2016,

had a second outcome. They worked as a recruitment base for sugar kelp seedlings, searching for empty substrate. The development in these frames were of further interest on our last visit in June 2017, as the recruitment occur during winter (Andersen et al., 2011).

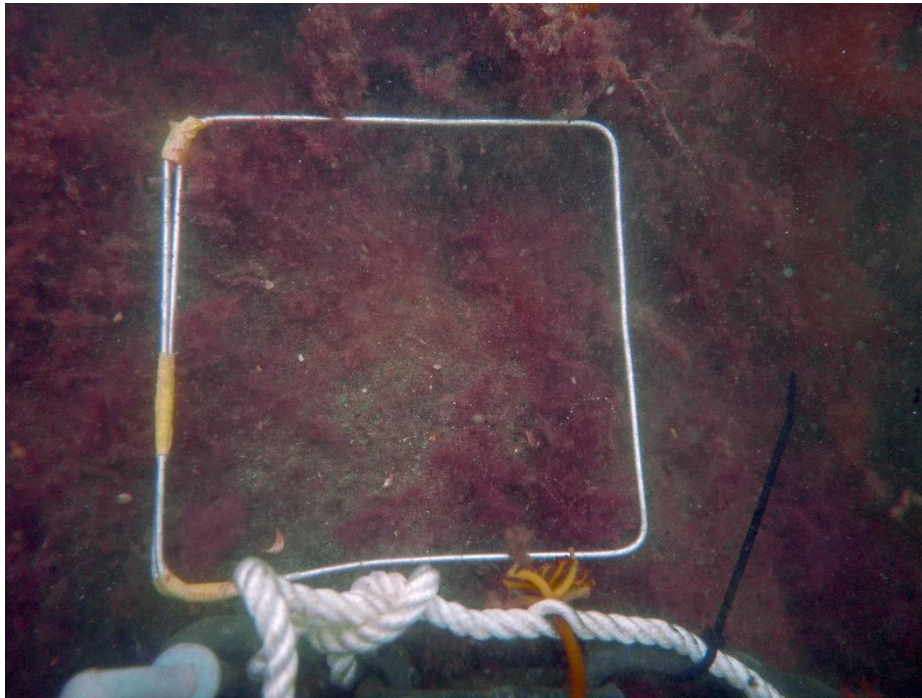


Figure 4: A 25 cm² frame was placed next to the transplanted sugar kelp and cleared. This was conducted in the same area at both surveys, summer and fall, in 2016. Photo: NIVA.

2.3.6 Pulse Amplitude Modulated (PAM) Fluorometry measurements

Pulse amplitude modulated fluorometry (PAM) is a nondestructive method of measuring photosynthetic performance (Hancke, 2007). The measurements were achieved by exposing the photosynthetic parts of the algae to a diode, which flashes it with different wavelengths of light, inducing fluorescence. The fluorescence represents the alga's ability to utilize the optimal wavelengths for photosynthesis, as the PAM-instrument measures the activity level in photosystem II (PSII). This gives an indication on the physiological state and well-being of the sugar kelp in

their particular territory (Brooks and Niyogi, 2011). *Ex situ* measurements was done using a diving PAM on deck in a boat. Measurements were done within short time to not reduce the physiological state of the plants, and the measurements were applied on two plants from stations, SA1 and SA3. Station SA1 is an exposed station, characterized by large fetch and good water circulation. Stations SA3 is more protected and is identified by calmer water conditions. Kasper Hancke from NIVA conducted the measurements during the survey in June 2016 (Fig. 5).



Figure 5: Photo illustrating how to measure the photosynthetic ability *in situ* with a Diving PAM-instrument. In this study, only *ex situ* measurements were taken. Photo: NIVA.

2.3.7 Laboratory analyses

The material from the cleared 25 cm² frame was analyzed in a laboratory at University of Oslo, using both a stereo microscope (Nikon SMZ-U zoom 1:10) and compound microscope (Nikon Eclipse E200). The different algal species in each sample were identified using the literature presented in Table 2. At the end, this generated a species list, presenting the species composition in each square at every station, for each of the two seasons, summer and fall 2016 (Table S1).

Table 2: Overview of literature used for identification.

Literature for species identification
Bestemmelsesnøkler til Rødalger, Jan Rueness, University of Oslo, 2006
Bestemmelsesnøkler til Brunalger, Jan Rueness, University of Oslo, 2006
Meeresalgen von Helgoland, P. Kornmann & P.-H. Sahling, Biologische Anstalt Helgoland Hamburg, 1977

2.4 Abiotic variables

2.4.1 Temperature

The temperature of the ocean has great implications for *S. latissima* as their optimum temperature ranges from 10 °C to 15 °C, and temperatures exceeding 20°C for an extended time may have severe consequences (Andersen et al., 2013). Due to this, measurements during the summer months were important. Temperature was recorded at every stations by using the HOBO® Pendant Temperature/Light Data Logger (Onset Computer Corporation, Massachusetts, USA), at 8 m depth. These recording-devices were fixed to a rope kept in place with a heavy weight on the bottom, and an empty bottle on the top to maintain a vertical position in the water column, one meter above the seafloor (Fig. 6). The temperature measurements were sampled from the 5th to the 25th of June 2016.

2.4.2 Light

Light conditions are fundamental for the growth of *S. latissima*. To uncover potential differences, The HOBO-loggers recorded the light intensity in units of lumen per square foot, also known as lux, which is the amount of visible light that reaches the sensor. The logger's main advantage is to illustrate changes and

differences, and this can give a good indication on the light conditions at each station. They recorded every ten minutes from the 5th to the 25th of June 2016.



Figure 6: The setup of the HOBO-logger, measuring the temperature and light conditions. The logger can be seen as the small white square tied to the rope, close to the vegetation (red circle). The air-filled bottle maintained a vertical position and prevented the device from being overshadowed by the flora. Photo: NIVA.

2.4.3 Sedimentation

The sedimentation cover has great implications for recruitment and tend to occur in combination with turf (Moy and Christie, 2012). The percentage cover of sedimentation was determined by eye sight using the same quadrat (1 m³) as in measuring the life stage of sugar kelp and turf cover.

2.4.4 Wave exposure

Modelled wave exposure index were obtained from a fetch model by NIVA (Isæus, 2004; Table S2). The wave exposure is modelled with 25 m spatial resolution as an index using data on fetch, wind speed and wind frequency. Fetch represents the shortest distance to the cost line or island in 16 directions (Isæus and Rygg, 2005).

Wind frequency is the amount of time a wind comes from a specific direction, while wind speed is measured in m/s and averaged over five years' period. Norwegian Meteorological Institute provided the wind parameters. The aim of measuring this parameter at each station, was to see if there is difference in wave exposure concerning the stations position among the skerries. This type of wave exposure model has been applied in many projects in Norway, Scandinavia and The Baltic (e.g. Bekkby et al., 2014; Isæus and Rygg, 2005; Norderhaug et al., 2012; Wijkmark and Isæus, 2010).

Table S2 provides the index and values from the Simplified Wave Model (SWM) classification. Based on these values, it is possible to view the study area and the stations in broader perspective (Table 3). Moreover, every station will be presented in accordance to wave exposure, from lowest (SA3) to highest (HB7), in all tables and figures.

Table 3: Overview of the conditions at each station, regarding wave exposure. SWM values provided by NIVA.

Station	Wave exposure	SWM index	Pointing position
HB7	Moderately exposed	118,662	West
SA2	Moderately exposed	116,949	Northeast
SA1	Sheltered	60,746	North
HB6	Sheltered	38,533	West
SA4	Sheltered	31,842	Northeast
SA3	Sheltered	22,119	East

2.5 Statistical analyses

2.5.1 Multivariate analysis

To analyze differences in the turf communities, multidimensional scaling was applied. The aim was to see if there was any clear pattern on how turf distribute along the coast. Thus, to see if there was a gradient regarding wave exposure. In classic ordination, one tries to simplify multivariate data by reducing it down from many dimensions to a few axes. This makes it possible to graph the observations and makes it easier to detect patterns. This will hopefully reflect the underlying biological processes. There are many types of ordination and in this case, Non-Metric Multidimensional Scaling (NMDS/Non-Metric MDS) would be a suitable treatment (cfr. Norderhaug et al., 2012). This type of ordination is a non-parametric method and it does not assume a linear relation between variables. NMDS arranges data-points based on dissimilarity, thereby giving them a rank-order. Data-points characterized by similar entities will be placed closer together in the graph than dissimilar data-points. This method is typical for species counts, and therefore useful for this study. Stations defined by similar species composition will appear closer together in the graph, while those stations composed of different species will emerge further apart (Clarke, 1993).

In the process of analyzing the factors affecting the presence of sugar kelp, it became apparent that several datasets were incomplete. This was mainly due to loss of transplanted sugar kelps or malfunctions of equipment. The lack of measurements at some seasons or stations made it difficult to utilize more advanced analyses, due to the lack of statistical strength. The deficient datasets were therefore presented in graph bars, illustrating their presence and not statistically analyzed. The missing data concerns mostly temperature measurements.

2.5.2 Univariate analysis

The main object of the statistical analysis was to identify the relationship between the response variable, and one or more explanatory variables. In this study, only the biological response recruitment was analyzed with univariate analysis, against the explanatory variables light, wave exposure and sedimentation. Survival, temperature and growth were not tested since the data do not meet statistical assumptions. Furthermore, it is recommended to regard these types of relationships as a generalized linear model (GLM) where the logarithm of the average response (i.e. the mean of the Poisson distribution) is a linear combination of the explanatory variables. The reason for taking the logarithm of the Poisson parameter is that the expected counting numbers necessarily must be a positive number, so a log-transformation takes both negative (mean less than one) and positive (mean greater than one) values. Thus the log-values may be modelled by a linear predictor with error terms having a normal distribution (linear regression model). In statistical terminology, this model belongs to the GLM-class with a Poisson distribution and canonical link function (Whitlock and Schluter, 2009).

In Poisson distribution, the aim is to see if events or objects appear randomly in time and space. It's based on count measure, and typically, the intention is to see if these counts vary within a habitat. The Poisson model assumes random events. Hence, the result become interesting when these assumptions are not met by the observation, and presents a pattern. The aim is therefore to look for number of success, and to see if these events are clumped. Ideally, this would indicate biological preferences or patterns within a habitat.

Since the recruitment is defined as the number of seedlings, the recruitment is measured as a natural number. For example, station SA1 has six recruits, SA2 has 186, while stations SA3 has zero recruits, in summer 2016. In statistical terms, this means that the response is a count variable with values among the positive integers (zero is as a non-negative number having a square root of 0, so technically we can regard zero as a positive integer). Thus, the recruitment is a count process.

However, the recruitment of marine organisms reproducing by spores is known to have a huge variability from year to year. In statistical terms this means that the recruitment is overdispersed. This implies that the variability is much greater than the average level, the mean. Since a Poisson variable has a variance equal to the mean, the overdispersion will lead to bias in the hypothesis testing. Overdispersion induces a higher probability of erroneously rejecting the null hypothesis. In order to avoid or reduce this problem, it is recommended to transform the response variable by extracting the square root. In the subsequent statistical analysis, recruitment is there for defined as the square root of the observed recruitment (Whitlock and Schluter, 2009).

In the process of further validation of the Poisson model, the square root recruitment was tested for normal distribution, heteroscedasticity and leverage. It is important to explore whether the assumptions of the regression model are valid, and decide whether the interference in the results of the statistical analysis can be trusted. In the linear regression model of the square root of recruitment versus a linear combination of station, season and sedimentation, it is assumed that the errors have the same variance. These are all assumptions in the GLM. The statistical program R (R Core Team, 2016) was used for univariate statistical analyses and the significant level was set to $P = 0.05$. Due to few samples of each factor, reducing their statistical strength, turf and wave exposure was analyzed in separate Poisson regressions. The factors temperature, survival, and growth of sugar kelp was not statistically analyzed and the data was treated using Microsoft® Excel 2016.

3 Results

Table 4 gives an overview of how each variable was analyzed. The relationship between the different variables was tested when they were supported by statistical strength, while those variables that had incomplete datasets are presented in graphs. The result chapter is structured after the environmental factors: temperature, light and turf & sedimentation. The biological responses: survival, growth and recruitment are presented according to its hypothesis, seen in Table 4.

Table 4: Overview of different analyses conducted on each factor.

Variable	Analysis	Hypotheses
Environmental	Temperature could have affected the presence of <i>S. latissima</i>	H1
Environmental	Light intensity varies, but does not affect growth	H2
Environmental	Light condition indicate an influence on recruitment (GLM)	H2
Environmental	Sedimentations effect on recruitment (GLM)	H3
Biological	Sedimentation cover influence the recruitment of <i>S. latissima</i>	H3
Biological	Turf composition indicate little difference among stations and exposure (MDS)	H3
Biological	Turf alter the recruitment of <i>S. latissima</i> (GLM)	H3

3.1 Temperature

The HOBO-logger equipped at every station recorded temperature and light, during June 2016. The temperature measurements were consistently too high when compared to the temperature measurements recorded by The Institute of Marine Research (IMR) in Flødevigen, Arendal (Fig. 7). It is seen that the

temperature measurement by the HOBO-loggers may deviate by such a large degree, that the data must be characterized as being beyond reasonable (Norderhaug pers. comm.). Continuous measurements from IMR provide calibrated temperature data every minute and all year round. Due to their near proximity (10 km) and similar conditions (inner coast) to the study area, these measurements from IMR in Flødevigen were used as our temperature recordings. The records were obtained from HI home pages.

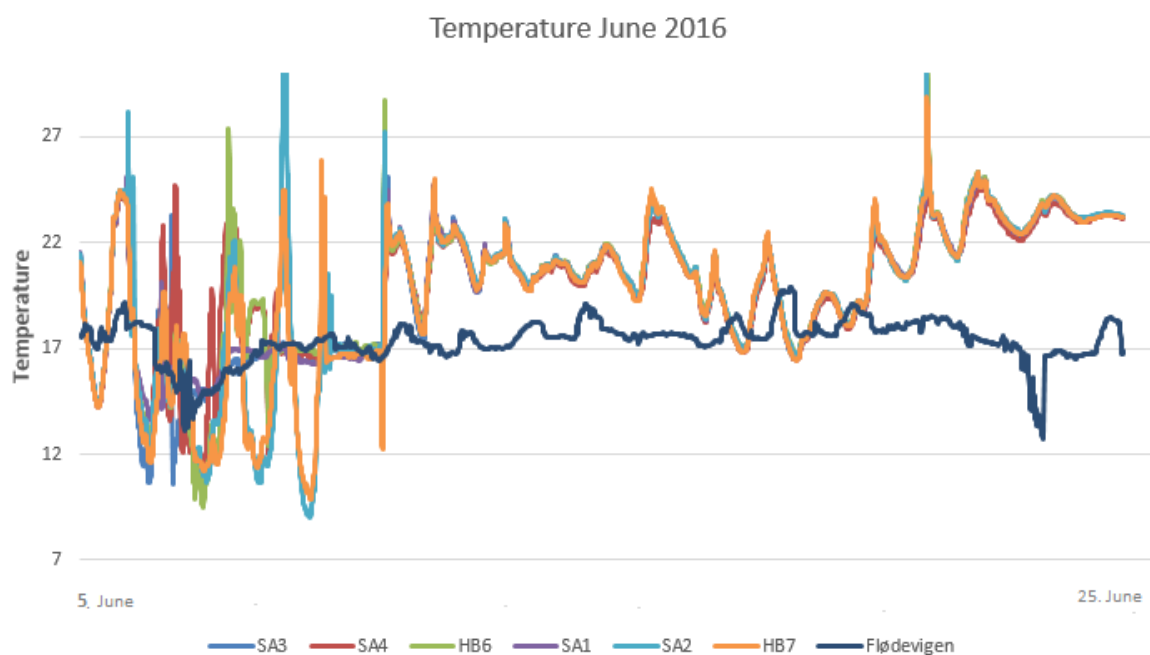


Figure 7: Temperature measurements from 5th to the 25th of June 2016. All lines, except the dark blue line, represents the stations from the study area. The dark blue line illustrates temperature measurements from Flødevigen, Arendal.

The temperature at Flødevigen varied between 12°C and 20°C at 1 m depth, in the period from June to October 2016 (Fig. 8). There were a few incidents when temperatures just exceeded 20°C, but this was only for a very short time period. During the same period in July, it was measured around 19°C for about

five to six days. During June 2017, when the last monitoring was conducted, the temperatures were continuously below 18 C° at 1 m depth (Fig. 8).

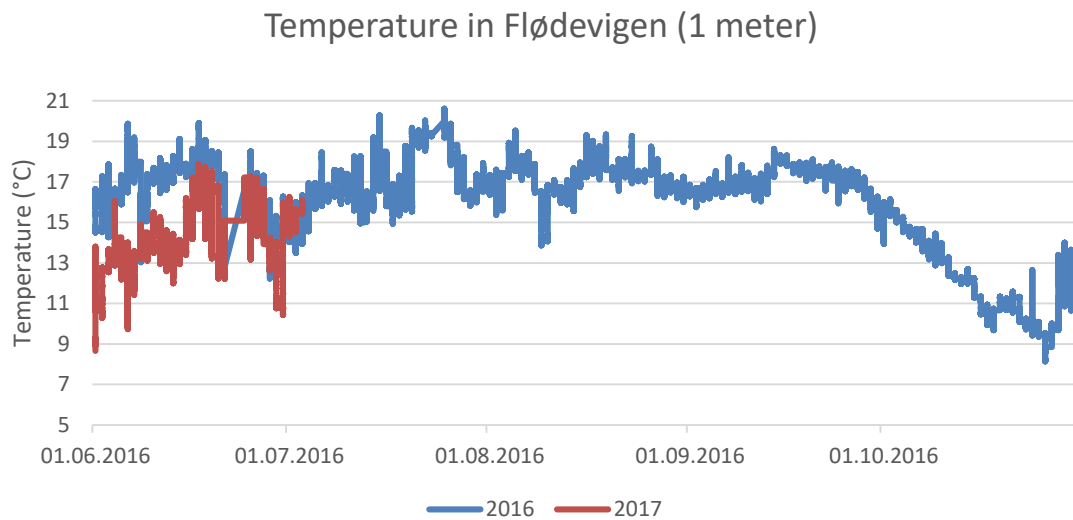


Figure 8: Temperatures at 1 m depth from June to October 2016 in Flødevigen, Arendal.

3.1.1 Survival

To investigate the biological response survival, the presence of *S. latissima* throughout the three seasons was counted. Analyzing these data in the light of temperature could give some information about the survival of *S. latissima*. However, due to the lack of temperature data from each station, it was not possible to perform statistical analyses. Only direct comparisons between the figures (Fig. 8 and 9) was possible.

The presence of different life stages of *S. latissima* varied between stations (Fig. 9). The most exposed stations had the highest presence of all life stages of sugar kelps, while the sheltered stations had a marginal presence of any life stages.

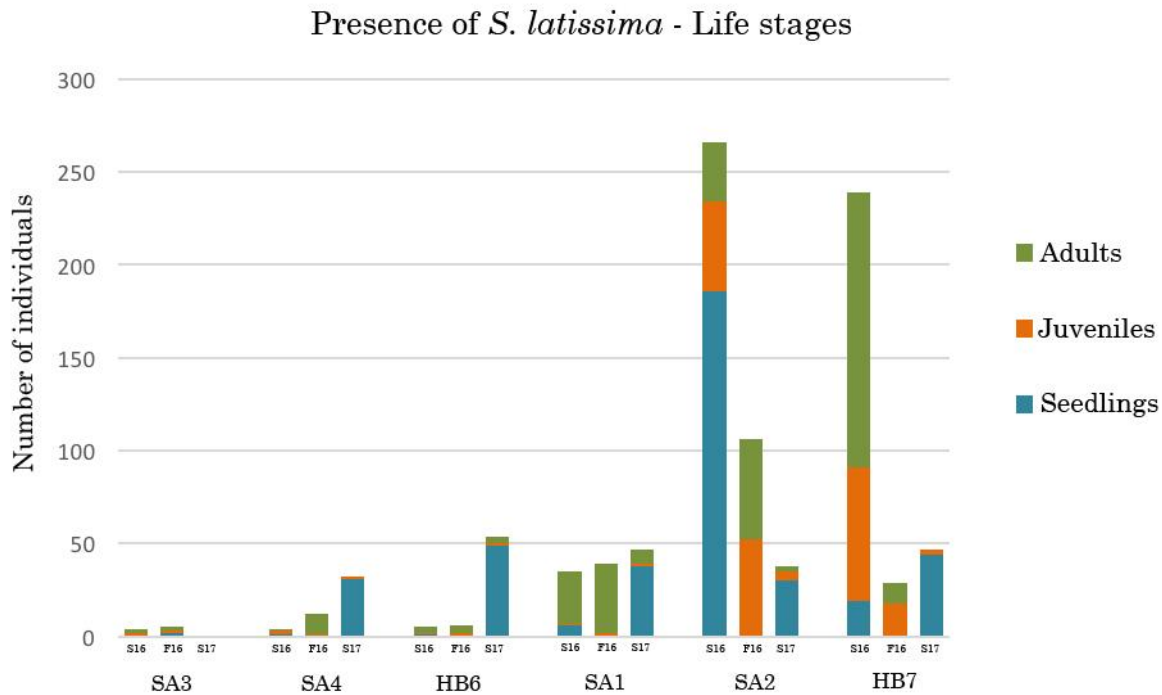


Figure 9: Presence of *S. latissima* in the different life stages. Each station includes three seasons; summer and fall 2016, summer 2017.

3.2 Light

Light availability varied from 218.69 lux (HB7) to 616.37 lux (SA4; Table S3). Higher values were found among inner and outer stations, and no gradient in light availability could be observed. Station SA4 and SA3 are among the most sheltered habitats, but the amount of available light was the highest at both stations. In contrast, station HB7 and SA2 had the highest wave exposure, but the lowest amount of light (Fig. 10). The presence of adult *S. latissima* is highest at the exposed stations, while the sheltered has a reduced or no presence. Recruitment has similar pattern, though less extreme.

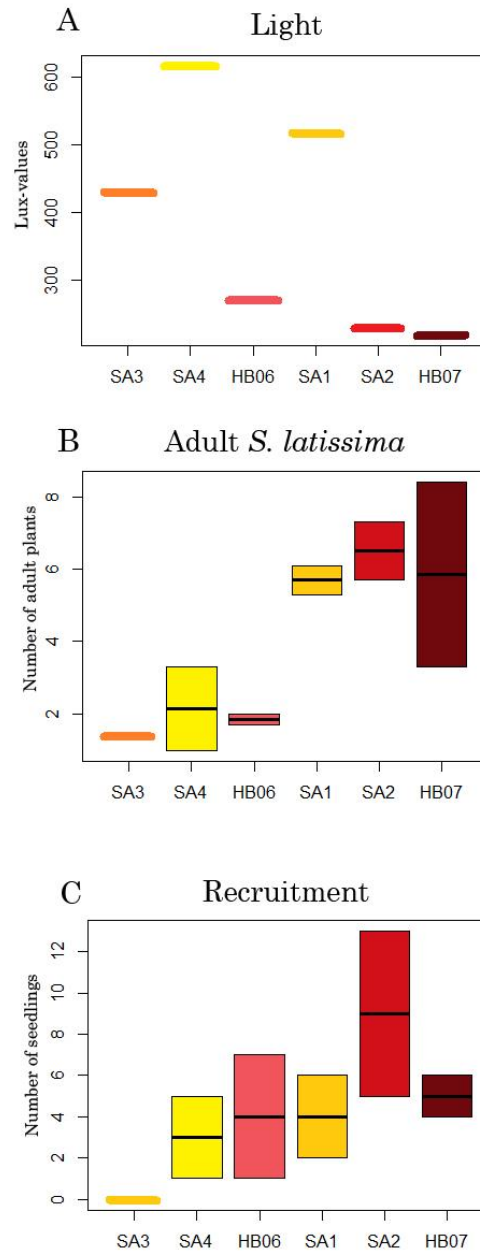


Figure 10: A) Overview of lux value at each station. B) Variability of adult sugar kelp each station in summer and fall 2016, and summer 2017. C) Variability of recruitment at each station in summer and fall 2016, and summer 2017.

The light availability had a significant P-value as an explanatory variable to recruitment, although the effect was nearly zero (Table 5).

Table 5: Overview of each model summary of every explanatory variable from the Poisson regression on recruitment (response variable).

Variable	Estimate	Std. error	Z-value	P-value
Turf	-0,08411	0,4650	-1,809	0,0705
Sedimentation	5,4411	2,1897	2,485	0,0130
Wave exposure	0,007053	0,001923	3,668	0,000244
Light	-0,002583	0,001049	-2,563	0,0138

3.2.1 Photosynthetic ability

Sugar kelps from both the inner and outer part of the skerries were tested for their photosynthetic ability. These measurements, using a diving-PAM, were conducted at station SA3 (inner coast) and at stations SA1 (outer coast), *ex situ*. The quantum yield (ϕ) of each plant lies between 0.6 and 0.7 (ϕ) (Fig. 11). Due to overlapping confident intervals (95%), there is no significant difference between the two algae in photosynthetic ability.

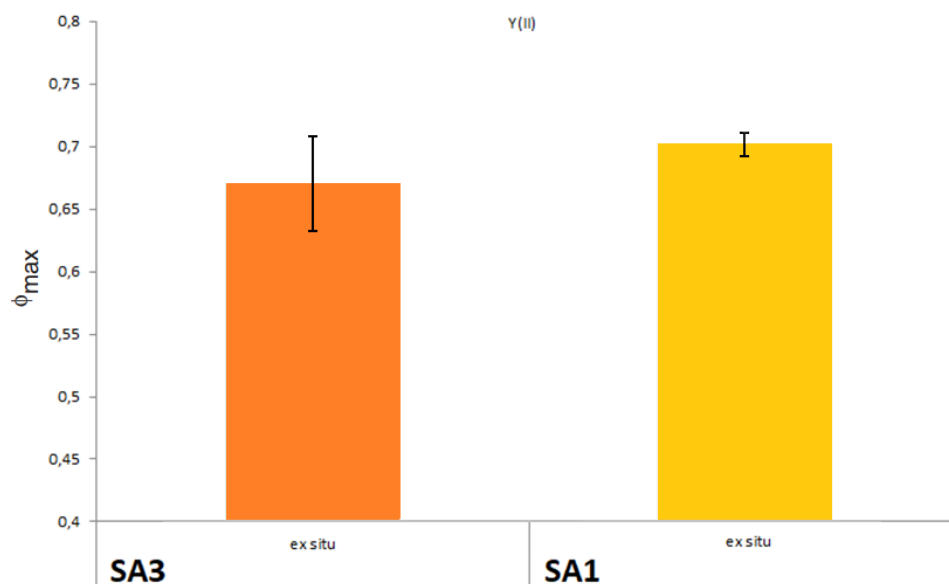


Figure 11: The quantum yield or photosynthetic ability of *S. latissima* on station SA3 and SA1 measured by Pulse Amplitude Modulated (PAM) Fluorometry. Each bar-plot are colored according to available light. Yellow indicates high lux-values, while orange imply lowered lux-value.

3.2.2 Growth

Most of the plants attached to the chain were lost throughout the experiment. Already after the second visit, fall 2016, 80% of the sugar kelps had disappeared. During the second sampling of the survey in October 2016, only 4 out of 30 individuals were still present. The four surviving individuals were still present on our last fieldtrip, summer 2017.

The stations with good light availability has three surviving sugar kelps (SA4 and SA3). These stations are characterized by reduced water movement (compared to HB7), being part of the inner skerries, and they have good light availability. The last surviving sugar kelp is on the most exposed station (HB7). This is also a station with low light availability. The growth rates of the surviving sugar kelps were quite similar (Fig. 12).

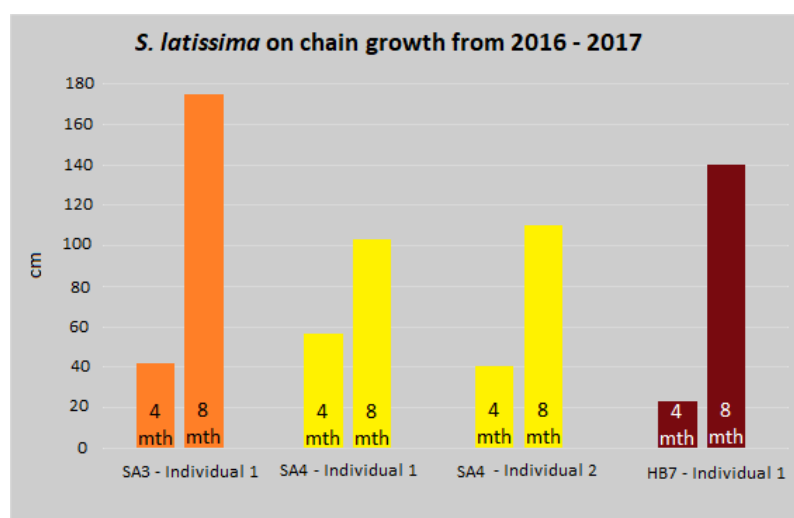


Figure 12: The growth in cm of surviving sugar kelp on chain. The first bar at each station represents the growth after four months, which encompass the period from summer to fall

2016. The second bar represents the subsequent growth from fall 2016 to summer 2017, encompassing an eight months' period. Coloration of each station correlates with lux-values, as seen in figure 10, and the order match their exposure level. SA3 is the least exposed station, while HB7 is the most exposed station.

3.3 Sedimentation and turf

Sedimentation and turf affects recruitment. The sedimentation at each station is presented in Table S3. The turf samples from the cleared frames revealed little differences in number and composition of species at each station (Fig. 13 and table 6-7). The variation in species composition is shown in Figure 14.

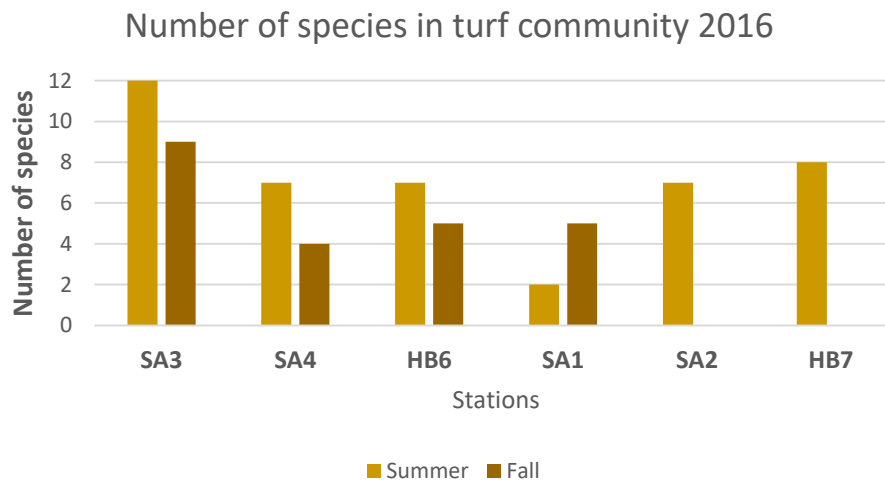


Figure 13: Overview of how many species found at each station, summer and fall 2016. Stations (SA2 and HB7) had empty routes, during the monitoring in fall 2016.

The samples collected during the summer season of 2016, gave little indication of any structural difference among the stations. *Brongiartella byssoides*, *Coccotylus truncatae* and *Sphacelaria cirrosa* were found in two out of three stations in the more protected area, while none of these species were found among the more exposed stations (Table 6). This is the main difference in species occurrence along the exposure gradient.

Table 6: Species list of the most frequent species from the cleared frames. For full species list see appendix.

Summer 2016	SA3	SA4	HB6	SA1	SA2	HB7
Species/exposure level	Lowest	Lower	Low	High	Higher	Highest
1. <i>Brongiartella byssoides</i>		X	X			
2. <i>Coccotylus truncata</i>	X		X			
3. <i>Sphacelaria cirrosa</i>	X		X			
4. <i>Bonnemaisonia hamifera</i>	X		X			X
5. <i>Dasysiphonia japonica</i>	X		X		X	
6. <i>Saccharina latissima</i> (juveniles)		X	X	X	X	
7. <i>Chondrus crispus</i>		X	X		X	X
8. <i>Desmarestia aculeata</i>	X	X			X	X
9. <i>Polysiphonia stricta</i>	X	X			X	X
10. <i>Corallina officinalis</i>		X	X	X	X	X

The difference in species composition in fall 2016 was also quite modest. *P. stricta* is the only species that was only found among the protected stations (Table 7). *B. hamifera* was more common in the inner skerries. Beside from this, very few species displayed any trend in appearance regarding location.

Table 7: Presence/absence of the most common species in the cleared frames from fall 2016. The list is based on the difference in species composition between the stations, from sheltered to more exposed habitat. Only species that differ are included in this list. For full a species list, see appendix.

Fall 2016	SA3	SA4	HB6	SA1	SA2	HB7
Species/exposure level	Lowest	Lower	Low	High	Higher	Highest
1. <i>Polysiphonia stricta</i>	X	X	X			
2. <i>Bonnemaisonia hamifera</i>	X	X	X	X		
3. <i>Desmarestia acuelata</i>	X	X	X			
4. <i>Ahnfeltia plicata</i>			X			
5. <i>Ceramium tenuicorne</i>	X					
6. <i>Sphacelaria cirrosa</i>	X					
7. <i>Chondrus crispus</i>	X				X	
8. <i>Corallina officinalis</i>			X	X		
9. <i>Dictyota dichotoma</i>					X	
10. <i>Polysiphonia</i> sp.					X	

The ordination diagram (MDS) based on species composition of turf communities illustrates little structure, with most markers scattered within the diagram. The only tendency of grouping can be seen among the exposed stations (see blue markers in Fig. 14). These stations are characterized by low diversity. The green markers lying horizontally out from these blue markers, are all characterized by lower exposure level. Thus, this could exhibit a horizontal gradient of exposure. The vertical spread of markers could demonstrate species composition. The weak cluster of stations (SA4s, SA2s and HB7s) consists of similar species, while the

vertical spread of markers from this area, have a wide range of different species. Hence, the wide spread of markers.

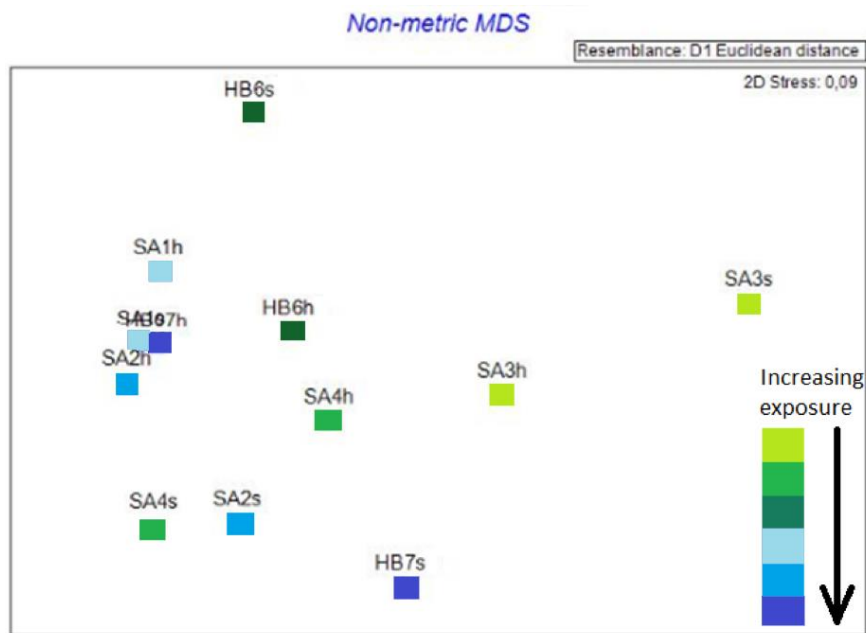


Figure 14: Ordination of the stations in regard to turf species. The diagram shows how different species of turf are distributed. The notation “s” and “h” at each mark indicate the season summer and fall, respectively. The color represents wave exposure, where green is low exposure and blue colors more exposed stations.

3.3.1 Recruitment

To get a visual impression of the covariability between the presence of the recruitment, the amount of sedimentation and turf cover, it was natural to start looking at a boxplot which gives an impression of these relation. Each boxplot, representing the stations, includes both summer seasons (2016 and 2017; Fig. 15). The stations are ordered according to wave exposure from lowest (SA3) to highest (HB7). Particularly noticeable is station SA3, which shows zero recruitment (Fig. 15 A) as well as 100% sedimentation cover (Fig. 15 C) and almost 100% turf cover (Fig. 15 B). The recruitments at stations SA2 and HB6 have a broad interquartile area, indicating substantial variability between the two summer seasons. However, most boxplots are overlapping (except SA3), so there are no

significant differences among the station, concerning recruitment (Fig. 15 A). Such huge variability can also be observed on the turf cover on station HB7 and SA1. Both stations have a large divergence on turf cover between summer 2016 and 2017 (Fig. 15 B).

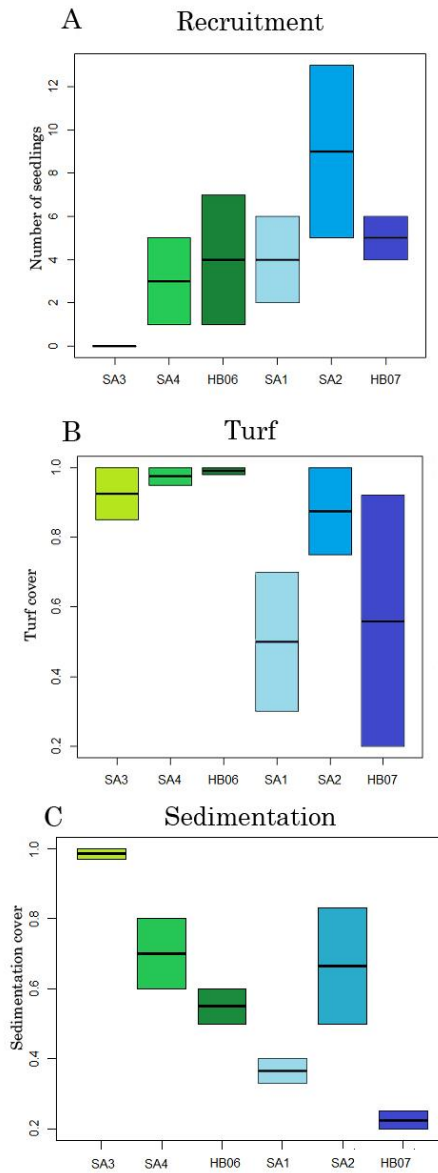


Figure 15: Boxplot from two summer seasons, 2016 and 2017. The stations are ordered according to wave exposure, where station SA3 has the lowest exposure and HB7 has the highest exposure, from light green to dark blue. (A) Boxplot of recruitment at each station. Y-axis indicates number of recruits (square root transformed data). (B) Boxplot of turf cover at each station. Y-axis indicate the turf cover in percentage. (C) Boxplot illustrating sedimentation at each station. Y-axis indicate sedimentation cover.

To investigate how sedimentation and turf affects the recruitment, and to get a statistical understanding of these relations, statistical treatments of the variables was performed. This was mainly to confirm that the data met the GLM assumptions. The observations show a left-skewed distribution because of the extreme recruitment at the exposed station (SA2). However, this is no sign of an aggregated pattern and the recruitment maintains an acceptable spread (Fig. S6). The residuals may be assumed to have a normal distribution and no observation seems to be an outlier. This indicates that there is no observation which has a strong influence on the regression line, and supports the conclusion of a linear relation between observed and expected observations (Fig. S7). To investigate this further, it is necessary to look at the leverage which measures the impact of the various observations on the regression model. In this analysis the stronger influence of stations SA2 was confirmed. This observation (SA2) has a stronger impact on the regression line (Fig. S8).

Sedimentation

In the process of finding which model that explains the observed variability in an adequate way, different factors were included in the two analyses conducted (S2 and S3).

In the first logistic regression (Fig. S2), sedimentation had no significant impact on the recruitment. When the various stations, seasons and sedimentation were added as explanatory variables, the model could explain much more of the variability in the recruitment (Fig. S3), and the Akaike information index was reduced from 74.5 to 54.3. The effect from sedimentation (Fig. S3) is depicted in Table 10. The positive sign of the sedimentation coefficient is due to the fact that in this model the sedimentation is put together with all the other parameters. Here we can see that sedimentation has a significant effect on recruitment. Station HB6 has been used as a reference (Fig. S3). This is a sheltered station with no recruitment and one can see that the other more exposed stations with present

recruits has a positive effect on recruitment. Moreover, exposure has a positive effect on recruitment.

Wave exposure

This indication was further approved by the separate analysis on wave exposure (Fig. S4). Wave exposure has a positive effect on the response variable, recruitment. The significance level is below 0.05 (P-value), which means that this parameter has a significant impact on the recruitment. The effect is small as the estimate is nearly zero.

Turf

The turf cover on each station, revealed weak difference with regard to recruitment. The data was incomplete, due to deficient sampling. The missing parts was replaced with data from turf community analysis. The model summary (Fig. S1) indicate weak influence of turf on the recruitment. The P-value is just above 0.05, which is not significant (Table 5). However, this still gives an idea of a weak correlation between the two factors.

After the collection of turf community in the cleared frames (25 cm³) in 2016, the subsequent outcome was to see if these clean substrates would facilitate recruitment for 2017. The outer stations, with high exposure level, were the only stations with recruits. This was station HB7 and SA1 (Table 8). These stations were only partly covered by turf, while stations on the inner coast were completely overgrown by turf.

Table 8: Recruitment of *Saccharina latissima* in cleared frames, June 2017. Data on turf cover, wave exposure levels and light availability for each frame (station) is provided in table. Stations with presence of recruits are colored in red.

Stations	Recruitment	Turf cover	Expose level	Light
SA3	0	100%	22.119	616,37
SA4	0	100%	31.842	519,91
HB6	0	100%	38.533	430,75
SA1	10	30%	60.746	269,05
SA2	0	100%	116.949	229,72
HB7	4	20%	118.662	218,69

4 Discussion

4.1 H1: Does high summer temperatures have a negative influence on *S. latissima* survival?

The temperature measurements from summer 2016 could have caused a potential threat to the survival of sugar kelp. The duration of warm temperatures (over 19°C) lasted for about a week, which could have made the sugar kelp vulnerable (Fig. 8). Moreover, there were less individuals in the quadrat measurements from summer 2017, than summer 2016 (Fig. 9). The results indicate that the increased temperatures could be one explanation to the 80% loss of individuals in the transplanted sugar kelps. Due to the failure of HOBO-loggers, it is difficult to conclude on any differences among stations. The temperature measurements from IMR are from 1 m depth which also limits the usage of these data, as every station was at 8 m depth. In the following season, June 2017, the temperature measurements never reached any high values, the highest maximum temperature being at 18°C (Fig. 8). The temperatures of the remaining summer were not relevant, as June 2017 was the last month of monitoring. This means that I cannot statistically conclude on the effect of summer temperatures of sugar kelp survival and further accept hypothesis 1.

As previously pointed out, when the Norwegian sugar kelp is kept at 20°C for a prolonged time (weeks), they start to show evidence of reduced fitness (Andersen et al., 2013). High temperature levels prevent adequate protein production of essential enzymes like PSII and Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), as well as maintenance of other important structures. The immediate outcome of this is reduced photosynthetic ability (Davison, 1991). Furthermore, the increased temperature leads to higher respiration which demands even more photosynthesis (Campbell et al., 2007). In these situations, the risk of decomposition increases, as the sugar kelp becomes less resilient against other stress factors.

Studies by Gerard and Du Bois (1988) and Gerard (1997) shows that sugar kelp from temperate climate were better able to acclimate increasing temperatures, than sugar kelp from slightly colder climate. Moreover, that sugar kelp in higher latitudes, were not well adapted for high summer temperatures, and lacked a necessary nitrogen-allocation strategy. This strategy involves the ability to accumulate high concentrations of nitrogen, and maintain this concentration under longer periods of low supply of nitrogen, i.e. under high temperatures. In a study by Andersen et al. (2013), it is further shown that the Norwegian sugar kelp are indeed not acclimatized and not able to withstand the increased photosynthetic performance needed under increased temperature. In the light of this, it can indicate that the Norwegian sugar kelp are more vulnerable to temperature, than more southern populations of the species. Moreover, this indicates that increased temperature, as a consequence of climate change, can be one of the main factors for the reduction in distribution of southern Norwegian *S. latissima*.

4.2 H2: Does poor light condition have a negative effect on *S. latissima* growth and recruitment?

The amount of incoming light at each station did not reflect a gradient, as expected (Table 3 and Table S2). One of the most sheltered stations, SA4, had the highest lux-value. This is opposite of what to expect. The sheltered stations are surrounded by more stationary coastal water, and such calm conditions implies that input of freshwater and particles remains to a larger degree. Thus, occluding the transparency. The most exposed stations, SA1 and HB7, had the lowest lux-values, when one could expect that these stations would be characterized by increased light conditions. In this study, *S. latissima* growth did not show any correlation to available light (Fig. 12), nor did recruitment (Fig. 10). Due to the lack of available data in this study, this cannot be used to answer hypothesis 2. The lux-results could be an artifact influenced by various factors that requires elaboration.

The reduced transparency at the exposed stations could be caused by sugar kelps itself, as these stations had the greatest presence of adult sugar kelp (Fig. 10). Large laminas could obstruct the HOBO-logger and reduce the actual light condition. Thus, contributing to an inaccurate measurement. Another explanation for lower light conditions in the exposed areas, could be sedimentation covering the HOBO-logger. In contrast to what was just postulated, the increased wave exposure could stir up particles which could partly block the recording device as the sediments accumulate. A third explanation could be the orientation of stations in relation to the sun. Station HB7 (east) and SA1 (west) are very close, but have an opposite orientation. This could potentially constitute a reason for their difference in recorded light availability.

The amount of available light has been gradually reduced in the southern Norwegian coastal waters (Moy et al., 2009). This has been an ongoing trend during the 20th century and has caused a proportionate reduction in sugar kelps depth distribution. The cause of the light reduction cannot be singled out, but one primary contributor is freshening of the coastal waters (Sætre, 2007; Sætre et al., 2003). Freshwater supply usually comes with a higher concentration of dissolved organic matter, in contrast to the coastal waters it enters. This is believed to be the main cause of the darkening effect (Aksnes et al., 2009). Another indirect effect of the freshwater supply is an increased concentration of nutrients and phytoplankton, as the nutrients carried by the freshwater could lead to algal blooms. This will only add to the effect of light attenuation as blooms will decrease the water transparency and obstruct the vital sun. All though *S. latissima* is adapted to low light conditions, especially in the Arctic (Dunton, 1985), they are very depended on this vital summer sun. Spring and summer is the time to build up carbon reservoirs for the upcoming winter (Kain, 1979). This critical time period of their life cycle is now becoming more unstable as eutrophic processes threatens *S. latissima* presence.

The results from this study indicate no significant difference concerning photosynthetic ability (Fig. 11). This means that adult sugar kelps in sheltered areas (SA3) with slightly reduced light influx, are equally able to utilize available

light as sugar kelp from more exposed area with an increased light availability (SA1). Both sugar kelps show adequate levels of maximum quantum yield lying between 0.6 and 0.7 (Φ max). This value is expected among healthy algae and indicate adequate photosynthetic ability (Hancke, 2007).

The PAM-result shows that the adult sugar kelp in Grimstad is in good physiological state, and that possible deviations in growth most be a result of external factors. All though many of the sugar kelps on chain were lost during the summer of 2016, the growth of the four remaining plants was good for the summer season (Fig. 12). All four plants grew between 0.3 – 0.45 cm a day⁻¹ during the season, which is similar to many other studies (Andersen et al., 2011; Davison, 1987; Reynolds, 1974). Growth during winter was considerable higher, which was expected considering this is the season for elongation (Kain, 1979). These few examples indicate that adult sugar kelp in Grimstad, grows equally good independently of their environmental differences.

The relatively great loss of individuals may have been caused by inadequate study design. Incomplete or poor attachment of sugar kelps to the chains could explain the great loss. This is even more likely on the most exposed sites, where friction from pounding waves will decrease their chance of anchoring. Water movements could also have caused substantial damage to the leafs if the kelp did not maintain an upright position. Such tearing and damages on the leafs from interaction with the rocky bottom would destroy photosynthetic parts, making the sugar kelp vulnerable. Moreover, the sugar kelps lamina could also have been heavily overgrown by epibionts during the summer and fall, which would further increase the drag from waves.

4.3 H3: Does turf and sedimentation have a negative effect on *S. latissima* recruitment?

Increasing amounts of sedimentation and elevated quantities of turf revealed a negative effect on the presence of *S. latissima* recruitment, thus accepting

hypothesis 3. However, the statistical analysis gave some ambiguous results (Fig. 15, Fig. S1). The main reason for these unclear indications are most likely due to low statistical strength caused by few samples of each variable. Figure 15 shows that sedimentation and turf decreases with increasing exposure, while the recruitment is opposite. Moreover, the model summary (S1 and S3) acknowledge these levels of correspondence, but the differences in P-value, indicates that turf has reduced statistical strength. The results are similar to the broad conception that the presence of sugar kelp on the inner coast is declining, and that turf and sedimentation accumulate easier in these calm areas (Andersen, 2013a; Moy and Christie, 2012; Norderhaug et al., 2015). Due to this, the relationship between recruitment and wave exposure was further analyzed in a Poisson regression, that gave additional verification (Fig. S4).

It is especially in the calm waters among the inner skerries that turf algae communities, loaded with sediments, really develops and prevent the settlement of spores (Andersen, 2013b; Moy and Christie, 2012). Furthermore, if the spores are able to settle, these juveniles could rapidly be covered in fast growing turf as the summer unfold. According to Andersen (2013), there is good production and dispersal of viable spores, so this is likely not the barrier for the recruitment.

There have been speculations regarding cascade effects, as top predators are being overfished. This will lead to more secondary consumers that feed upon the grazers (Moksnes et al., 2008). Less grazers leads to more turf and epiphytes that will overgrow the kelp.

Again, this is most prominent among the inner skerries, with less water exchange and shallower conditions (Moy and Christie, 2012). It has been discussed that the invasion of turf in many ecosystems, could represent a new alternative stable state, being difficult to reverse (Scheffer et al., 2001). Sugar kelp struggles to recolonize lost areas, especially on the inner coast, while on the outer skerries a more successfully recolonization has been observed. (Moy and Christie, 2012).

The results from the composition of turf communities did not reveal significant difference along the exposure gradient, though there were a few species that

seemed to appear more often in one area (sheltered/less sheltered; Table 6 and Table 7). This seems to be connected to season. The difference was most remarkable in the fall, which could have been caused by the turf development during the summer. In early summer, it was observed in many stations, that some turf algae like *Polysiphonia stricta*, *Bonnemaisonia hamifera* and *Desmarestia acuelata* were able to establish. They could have lost this position when nutrients decreased throughout the summer, and the altered level of exposure would physically tear them away over time. Thus, only appearing on the most sheltered stations at the end of the season (Table 7). The three species mentioned above are quite common in sheltered coastal waters (Eriksson et al., 2002). Another factor to consider in this perspective, is the missing samples from fall 2016, on station SA2 and HB7. The absence of these samples could be misleading regarding which turf algae that actually appear on these stations for the particular season (fall).

The reduction in number of species in the turf communities from summer to fall is also reflected in the MDS diagram (Fig. 14). This trend is expected as the turf communities decline or perish in the winter (Whittick, 1983). Similar trends were observed in Norderhaug et al, (2012), but in this study the differences in macrofaunal communities, based on season and exposure, displayed a more obvious distinction (Norderhaug et al., 2012). The lack of this in the current study, might be caused by few samples.

Sugar kelp's morphological adaptation promotes a stable environment, producing a kelp forest excellent for shelter and nursery for marine life (Christie et al., 2009). Physical stress imposed by wave action can even improve the species richness on kelp forests, by excluding competition of superior species (Norderhaug et al., 2012). If competitors within a limited space have a strong overlap regarding their fundamental niche, co-existence will be unstable and one of the competitors is likely to lose (Lotka, 1932; Volterra, 1928). This implies that wave surge could have beneficial outcomes in respect to diversity.

Within the inner skerries, water mass appears more stable. Factors such as temperature and river outflow can constitute a considerable difference. The input

of fresh water from river systems improves stratification, and together with reduced wave exposure it helps making the inner coast more susceptible for changes, especially regarding temperature and nutrient concentration (Bathen, 1968). These circumstances could favor turf over sugar kelp, as the annual algae thrive in eutrophic waters (Munda, 1993).

4.4 Further remarks

The sugar kelps once broad niche is now much smaller and their presence is oppressed in a changing environment. Global climate change and eutrophic processes is an ongoing trend, threatening kelps all over the globe (Filbee-Dexter and Wernberg, 2018). This could incite a pole-ward shift, making southern Norway a less preferred area for *S. latissima* (Müller et al., 2009). The current study acknowledges this trend. Adult sugar kelp might be better able to handle increased competition from turf and reduced light. However, young seedling seems to struggle to a greater degree, especially on the inner coast. This is a vulnerable and critical stage of their life cycle, and if further threatened, sugar kelps presence in southern Norway could be uncertain. Therefore, refuge habitats from adult sugar kelp may be crucial for the supplying of spores for kelp recruitment. A loss of these kelp communities would be misfortune for Norwegian coastal biodiversity. These ecosystems do not only benefit the biodiversity and the marine systems, but also human recreational activities and business. Norway as an old fishing nation are depended on a sustainable marine ecosystem to maintain healthy fish stocks. This cannot be taken for granted in such a changing environment (Norderhaug et al., 2015).

Forest regeneration of sugar kelp through facilitation of natural recolonization may be feasible because remnant healthy stands still exist (Andersen, 2013b). Whether the present-day bottom conditions permit kelp recruitment in the deforested areas remains uncertain, but in terms of favorable conditions, this should be possible (Moy and Christie, 2012). The turf community's success, and the sugar kelps retreat may represent an alternative stable state under the ambient

environmental condition (Kennelly, 1987; Scheffer and Carpenter, 2003). However, in the most recent year there has been observed a weak trend of improvement, in terms of recovery, in many areas along the southern coast of Norway (Moy et al., 2017). This is a small, but positive development.

5 Conclusion

H1: High summer temperatures has a negative influence on *S. latissima* survival.

It is seen in this study, that temperatures may have affected the survival of *S. latissima* in a negative matter. This is due to the week of high temperatures in July 2016, following a high decrease in abundance in sugar kelp summer 2017. However, due to possible malfunctioning of temperature recordings among stations, these data had to be excluded from the analysis. Moreover, the temperature data that was used from Flødevigen are taken at 1 m depth, while the stations are at 8 m depth. This can therefore lead to misleading data, and no conclusions can be drawn concerning the hypothesis 1.

H2: Poor light conditions have negative effects on *S. latissima* growth and recruitment.

There was no structure in the light measurement data, and it did not correspond to either growth nor recruitment. At stations with lowered light conditions, there were no sign of decreased growth or recruitment. Thus, light conditions cannot explain the decreased abundance of the sugar kelp in Grimstad. Hypothesis 2 can therefore be rejected based on this study.

H3: Turf and sedimentation has negative effects on *S. latissima* recruitment.

Both sedimentation and turf had a negative effect on recruitment. It was observed that when sedimentation and turf increased, the amount of recruitment declined. Sedimentation had stronger statistical strength than turf. However, there are large variations on turf and this gives unambiguous indications on what the true effect turf adds, based on this study. Neither the less, both of these factors showed to have a negative effect on recruitment, leading to acceptance of hypothesis 3.

6 Future studies

The data collected in this study revealed observation with uncertainty. This was mainly due to few sample, thereby low statistical strength. The first priority in a similar study would be to up-scale dimensions with more samples, and ideally in multiple fjords/skerries. Such in-depth study on the differences between inner and outer skerries could reveal a broader trend, and reduce the impact of local variability.

The adult sugar kelp in this study displayed equal growth in both sheltered and exposed areas. This was only a few individuals and a more extensive study on this, with more individuals could exhibit greater certainty on this trend.

Investigate the origin of sedimentations. What is the ratio between marine and land originated particles? Input of long-distance transported nutrients and particles has been reduced and local input constitute the dominating supply. Greater knowledge on local conditions is therefore important to reduce human impact from urbanization and agriculture.

The PAM-measurements in this study was only taken *ex situ* and only at two stations. It is needed to do these measurements *in situ* to monitor the photosynthetic ability in their natural environment.

7 Literature

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8 Appendix

Table S1: Complete overview over all species found in the cleared frames.

Table 4: Complete overview over all species found in the cleared frames			
SA3		SA4	
Summer	Fall	Summer	Fall
<i>Bonnemaisonia hamifera</i>	<i>Bonnemaisonia hamifera</i>	<i>Brongiartella byssoides</i>	<i>Bonnemaisonia hamifera</i>
<i>Ceramium cimbricum</i>	<i>Ceramium tenuicorne</i>	<i>Chondrus crispus</i>	<i>Desmarestia aculeata</i>
<i>C.tenuicorne</i>	<i>C. tenuicorne</i>	<i>Cladostephus spongiosus</i>	<i>Gracilaria gracilis</i>
<i>Coccotylus truncata</i>	<i>Chondrus crispus</i>	<i>Corallina officinalis</i>	<i>Polysiphonia stricta</i>
<i>Dasysiphonia japonica</i>	<i>Dasysiphonia japonica</i>	<i>Desmarestia aculeata</i>	
<i>Delesseria sanguinea</i>	<i>Desmarestia aculeata</i>	<i>Heterosiphonia plumosa</i>	
<i>Desmarestia aculeata</i>	<i>Phycodrys rubens</i>	<i>Polysiphonia stricta</i>	
<i>D. viridis</i>	<i>Polysiphonia stricta</i>		
<i>Polysiphonia elongata</i>	<i>Sphacelaria plumula</i>		
<i>P.stricta</i>			
<i>Pterothamnion Plumula</i>			
<i>Sphacelaria cirrosa</i>			
HB6		SA1	
Summer	Fall	Summer	Fall
<i>Bonnemaisonia hamifera</i>	<i>Ahnfeltia plicata</i>	<i>Corallina officinalis</i>	<i>Bonnemaisonia hamifera</i>
<i>Cladostephus spongiosus</i>	<i>Bonnemaisonia hamifera</i>	<i>Fucus serratus</i>	<i>Chondrus crispus</i>
<i>Corallina officinalis</i>	<i>Corallina officinalis</i>		<i>Corallina officinalis</i>
<i>Dasya siphonia</i>	<i>Polysiphonia stricta</i>		<i>Dictyota dichotoma</i>
<i>Delesseria Sanguinea</i>	<i>Sphacelaria plumosa</i>		<i>Polysiphonia sp.</i>
<i>Polysiphonia stricta</i>			
<i>Striaria attenuata</i>			
SA2		HB7	
Summer	Fall	Summer	Fall
<i>Akrosiphonia arcta</i>	Empty	<i>Bonnemaisonia hamifera</i>	Empty
<i>Chondrus crispus</i>		<i>Chondrus crispus</i>	
<i>Corallina officinalis</i>		<i>Chorda filum</i>	
<i>Dasya siphonia</i>		<i>Corallina officinalis</i>	
<i>Desmarestia aculeata</i>		<i>Delesseria sanguinea</i>	
<i>Polysiphonia stricta</i>		<i>Desmarestia aculeata</i>	
<i>Rhizodoniom tortuosum</i>		<i>Polysiphonia stricta</i>	
		<i>Ulva lactuca</i>	

Table S2: The wave exposure index is model based on fetch, wind speed and wind frequency (Isæus, 2004).

Wave exposure index	SWM value
Extremely exposed	2,000,000 – 5,000,000
Very exposed	1,000,000 – 2,000,000
Exposed	500,000 – 1,000,000
Moderately exposed	100,000 – 500,000
Sheltered	10,000 – 100,000
Very sheltered	4,000 – 10,000
Extremely sheltered	1,200 – 4,000
Ultra sheltered	1 – 1,000

Table 3: List of the lux-values of each station from the HOBO-logger.

Stations	lux S2016
SA4	616.37
SA1	519.91
SA3	430.75
HB6	269.05
SA2	229.72
HB7	218.69

Table S4: Sedimentation cover

S2016	H2016	S2017
0.97	1	1
0.8	1	0.6
0.6	1	0.5
0.33	0.35	0.4
0.83	0.8	0.5
0.25	0.1	0.2


```

Call:
glm(formula = sqrtrec ~ turf, family = poisson, data = recsed)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.7926  -1.5874  -0.1836   0.7888   3.4064

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  2.0758     0.3700   5.611 2.02e-08 ***
turf        -0.8411     0.4650  -1.809  0.0705 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 40.274  on 11  degrees of freedom
Residual deviance: 37.247  on 10  degrees of freedom
AIC: 73.626

Number of Fisher Scoring iterations: 5

```

Fig. S1: GLM summary of the squared recruitment (response variable) modeled by turf cover (explanatory variable). The p-value for turf is higher than 0.05, thereby indicating that the turf had no significant impact on recruitment.

```

Call:
glm(formula = sqrtrec ~ sedimentation, family = poisson, data = recsed)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.4387  -1.6062  -0.2114   0.4947   4.0074

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.8783     0.3313   5.669 1.44e-08 ***
sedimentation -0.8128     0.5664  -1.435  0.151
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 40.274  on 11  degrees of freedom
Residual deviance: 38.158  on 10  degrees of freedom
AIC: 74.536

Number of Fisher Scoring iterations: 6

```

Fig. S4: Model summary of sedimentations effect on recruitment. In this analysis sedimentation is the only factor included, in contrast to the analysis conducted in Fig S3.

```

Call:
glm(formula = sqrtrec ~ ., family = poisson, data = recsed)

Deviance Residuals:
    1     2     3     4     5     6     7     8
-0.00006  -1.23112  -1.17346   0.54366   0.44553   0.69690  -0.00013   0.91709
    9    10    11    12
 0.69023  -0.26535  -0.62883  -0.47389

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -3.5171     1.9201  -1.832   0.0670 .
stationHB07    1.9383     0.8271   2.343   0.0191 *
stationSA1     0.7691     0.5623   1.368   0.1714
stationSA2     0.2049     0.5115   0.401   0.6888
stationSA3    -23.0491    6107.6590  -0.004   0.9970
stationSA4    -1.0480     0.6183  -1.695   0.0901 .
sedimentation  5.4411     2.1897   2.485   0.0130 *
season         1.2349     0.4962   2.489   0.0128 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 40.2737  on 11  degrees of freedom
Residual deviance:  5.8803  on  4  degrees of freedom
AIC: 54.259

Number of Fisher Scoring iterations: 17

```

Fig. S3: Model summary of Poisson regression on the square root recruitment. In this model every station, sedimentation and the season is applied as explanatory variables.

```

Call:
glm(formula = sqrtrec ~ exposure, family = poisson, data = recsed)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.9264  -1.1830  -0.9172   1.2094   2.2622

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.432805   0.564344  -0.767 0.443131
exposure     0.007053   0.001923   3.668 0.000244 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 40.274  on 11  degrees of freedom
Residual deviance: 25.842  on 10  degrees of freedom
AIC: 62.22

Number of Fisher Scoring iterations: 5

```

Fig. S4. Model summary of the impact of wave exposure on recruitment. The explanatory factor (wave exposure) has a significant impact on the recruitment.

```

Call:
glm(formula = sqrtrec ~ Light, family = poisson, data = recsed)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.6096  -1.2005  -0.3792   0.9946   2.6033

Coefficients:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  2.337905   0.370661   6.307 2.84e-10 ***
Light        -0.002583   0.001049  -2.463  0.0138 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 40.274  on 11  degrees of freedom
Residual deviance: 33.566  on 10  degrees of freedom
AIC: 69.944

Number of Fisher Scoring iterations: 5

```

Fig. S5: Model summary of the effect of light conditions of recruitment. Light has a significant impact on recruitment with a p-value below 0.05.

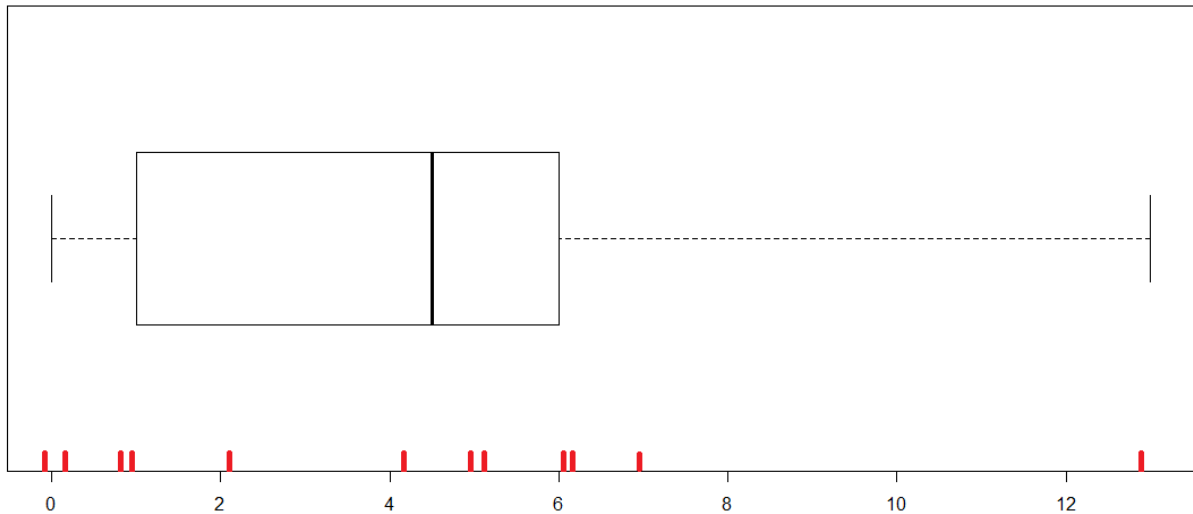


Fig. 6: A jittered boxplot of the recruitment from each station (data square root transformed). The box extends from the 25% to 75% percentile of the distribution, with the vertical line representing the median value (50% percentile). The whiskers outside the box represents the minimum and maximum recorded recruitment. The small vertical red lines on the x-axis represents the observed number of recruits (square root transformed) at each station.

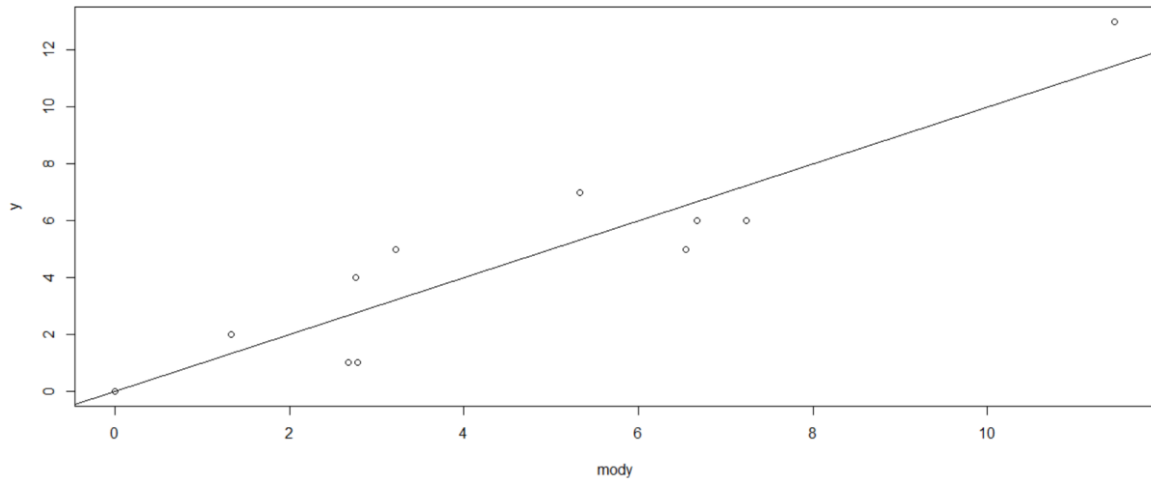


Fig. S7: QQ-plot of the residuals of square root recruitment. Note that the points cluster around the straight line $y = x$ which give a qualitative indication that the assumption of normality of the model errors is acceptable.

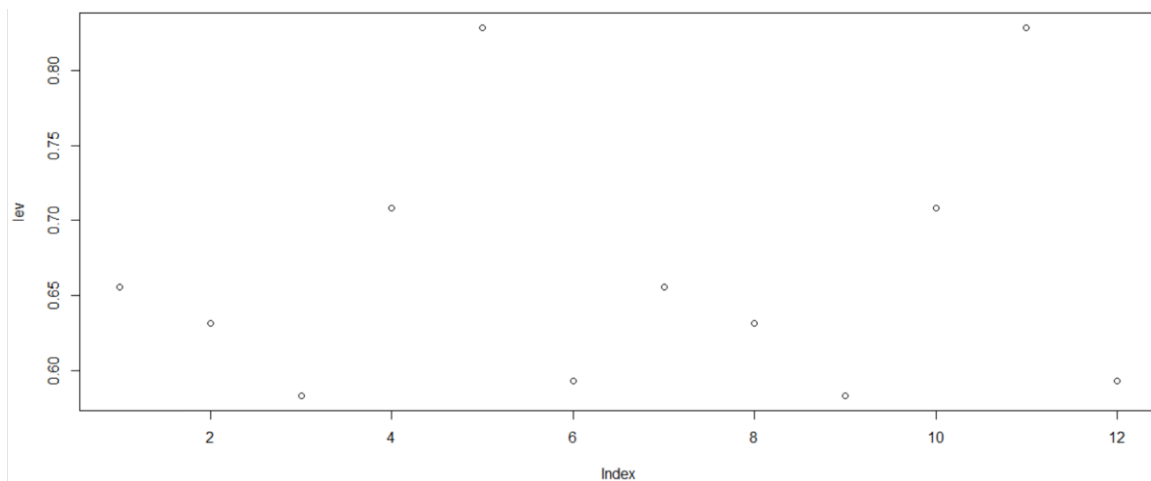


Fig. 8: Leverage analysis of each observation (recruitment). It is seen that the four points (SA2, SA1 one for each of the two seasons 2016 and 2017) have a large leverage and therefore have a significant influence on the regression model.